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BIOLOGICAL BULLETIN

THE REACTIONS OF CERTAIN ANIMALS TO GRADIENTS OF EVAPORATING POWER OF AIR. A STUDY IN EXPERIMENTAL ECOLOGY.

VICTOR E. SHELFORD.

WITH A METHOD OF ESTABLISHING EVAPORATION GRADIENTS BY
V. E. SHELFORD AND E. O. DEERE.

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I. INTRODUCTION.

Aside from studies of the hygienic workers (Rubner and others), studies of mountain sickness, and other physiological phenomena of high altitudes and reduced atmospheric pressure (Cohnheim and others), little attention has been given to the effect of loss of water upon land animals. Since evaporation is determined by air movement, humidity, pressure, temperature, and indirectly by illumination, most of the so-called physical factors are measured in combination by instruments measuring evaporation.

A knowledge of the effect of evaporation upon animals is important for the following reasons: (1) Because knowledge of the relationships of land animals to the surrounding medium is important from the standpoint of evolution and physiology, (2) because factors controlling distribution are effective in proportion to their effect upon the organisms concerned, and (3) because animals kept under laboratory conditions in experiments in behavior, genetics, etc., are often subjected to constantly changing atmospheric conditions and these changes may be sufficiently important to interfere with the results and the validity of the conclusions drawn. With these points in mind, the writer and Mr. E. O. Deere undertook to construct a piece of apparatus for the control of atmospheric conditions, but especially to establish experimental gradients and to test the reactions of animals to variations in the rate of evaporation. Various difficulties were experienced in getting the apparatus into working order and it was necessary for Mr. Deere to leave when the apparatus was ready for the control of humidity and some half dozen experiments had been performed. Nearly all of the experiments accordingly devolved upon the writer and we present the method of work only, as a joint contribution.

II. A METHOD OF ESTABLISHING EVAPORATION GRADIENTS.

BY VICTOR E. SHELFORD AND E. O. DEERE.

The air supply was obtained by a compression pump as shown in Fig. 1. A metal funnel (*MF*) covered with cheese cloth conducted the air to a pipe, 14 cm. in diameter and 340 cm. long, to a Beach-Russ Vacuum pump, no. 1, run by a one-half horse-power motor. The air left the pump through a $\frac{3}{4}$ -in. iron pipe, and entered a $\frac{1}{2}$ -in. Crane oil separator, which removed the oil with which the pump is operated. In the pipe near the oil separator there was a pressure gauge, an air-cock opening to the exterior, and an automatic blow-off set for 5 lb. pressure. From here the air passed through 15 m. of $\frac{3}{4}$ -in. galvanized iron pipe, the central 5 m. of which was surrounded by a $1\frac{1}{2}$ -in. iron pipe water-jacket, connected with the city water supply by means of a $\frac{1}{4}$ -in. iron pipe, provided with a valve. By turning the city water supply into this jacket we were able to lower the temperature of the air when the outside air was warmer than the room. This was necessary because after the flows were divided they passed varying distances before reaching the tanks and if the temperature of the air was higher than that of the room, different amounts of cooling gave different temperatures in the experimental boxes. Several brass ground unions made it possible to take the entire line apart. The air current was divided into six parts by means of iron pipe Y bends, and reduced to $\frac{1}{4}$ -in. with bushings. Each branch was provided with a

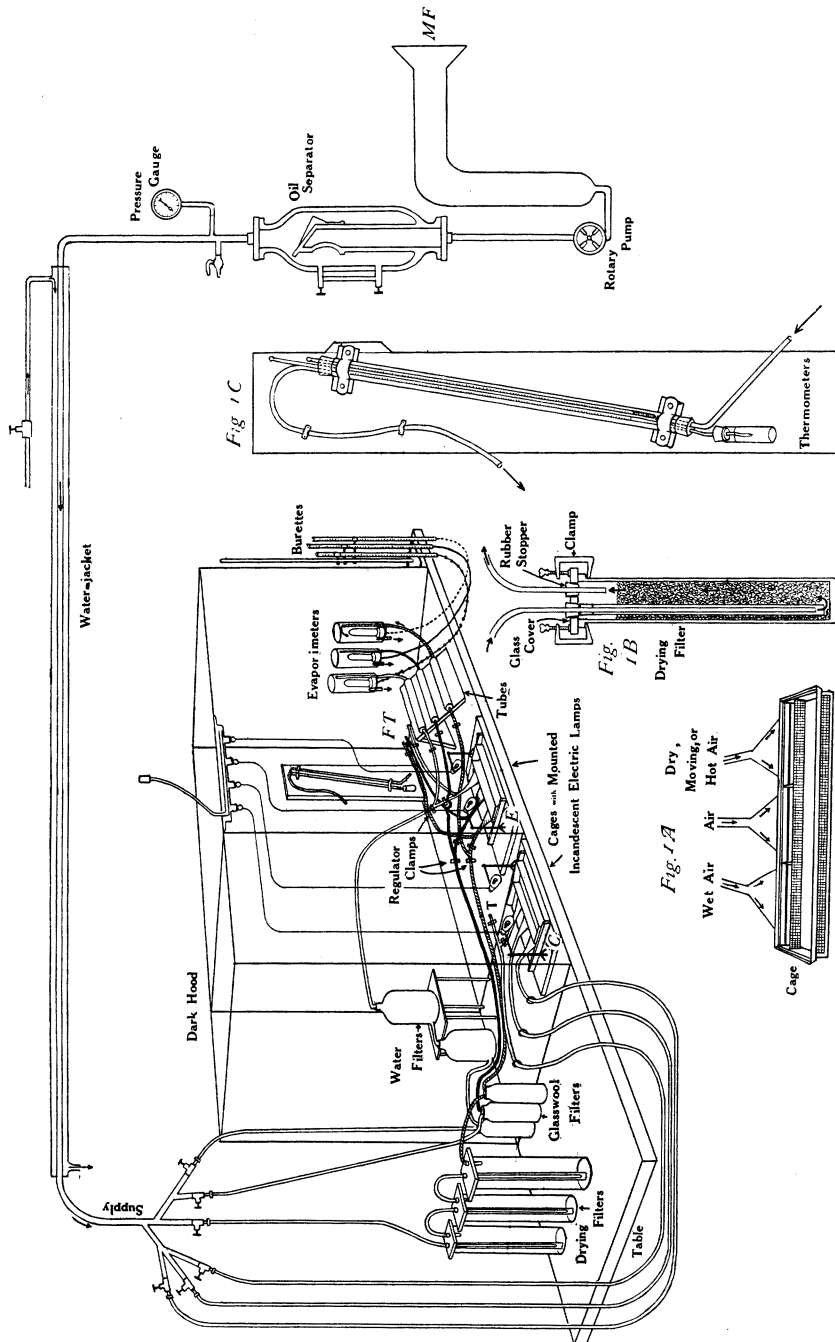


FIG. 1. Showing the apparatus for the control of the evaporating power with enlarged drawings of an experimental cage (Fig. 1A),—a drying filter (Fig. 1B), and the wet and dry bulb thermometers (Fig. 1C). MF is the metal funnel intake; T, a tube connected directly with the pump which may be connected with any of the tubes marked FT, directly or with a heating coil interposed. C is the control cage; E, the experimental cage. The latter is supplied with air from the various filters. For further description see text.

rising-stem straight-way valve, with hose end nipple attached by means of a $\frac{1}{4}$ -in. brass ground joint union.

The experimental boxes (Fig. 1A) for the gradient experiments were designed by the senior author and were 6.5 cm. wide by 30 cm. long, and 2.5 cm. deep. The animals were confined in a portion of each box, 5 cm. wide, by a screen (8 meshes to the centimeter). Air was supplied to the boxes by means of three fish-tail burner-shaped introducers, opening into a narrow slit along the rear midway between top and bottom. The area of the slit in each introducer was approximately the same as the area of the 7 mm. brass tube which connected it with the pump. The air after leaving the fishtail burner-shaped introducer passed through the screen that confined the animals away from the slit, across the box, and out of the front through a screen similar to the first. The air tended to spread out at about the angle of the side of the introducer, and a small piece of metal was inserted between the rear wall and the confining screen, to deflect this part of the flow directly across the box. Each experimental box rested upon a movable board to each end of which a ring stand was fixed. Each ring stand bore a universal clamp, a small piece of Bessemer rod, and a single burette clamp used to hold a 1 candle-power incandescent lamp in any desired position. Our experiments were performed with the center of the incandescent filaments 20 cm. from the bottoms of the experimental boxes, and one fourth of the distance from each end. These boxes were placed in a hood painted dead black, and provided with two curtains, one of which hung from above downward and contained a small slit for the observer, the other when in position came up from below to a point 10 cm. above the level of the lamp. This excluded practically all the faint light of the room, and the light was between the animals and the observer which made it less easy for them to see him.

The control box (C) was supplied either with untreated air direct from the pump or with no air. The experimental box (E) and Fig. 1A, when experiments with atmospheric humidity were being performed, was supplied with three kinds of air, wet at one end, dry at the other, and untreated or medium air in the center. The dry air was rendered dry by passage through three or more sulphuric acid filters, Fig. 1B (see Shackell, '09). Each filter consisted of a Whitehall Tatum museum jar, 45 cm. tall and 9 cm. in diameter at the top. The covers were pieces of plate glass, 13 mm. thick and provided with two holes 25 mm. in diameter. They were clamped into place by ordinary hardware screw-clamps with a 6 cm. opening. The contact points were filed smooth and covered with rubber tubing. The air entered through a glass tube inserted in a rubber stopper in one of the two holes in the cover just mentioned. In order to conduct air to the bottom of the jar, the tube through which it entered was inserted into a second cork fitting inside a larger tube (Fig. 1B) so that when the glass plate was pushed into place, this stopper was pushed inside the glass tube so as to make an air-tight connection. The air left the filters from the top through a short tube inserted in the second rubber stopper. The filter jars were filled with crushed pumice stone, the pieces ranging from 0.5 mm. to 7 mm. in diameter, as indicated by the meshes of the screens used in separating and removing the finest and coarsest pieces. This was impregnated with crude sulphuric acid.

After leaving the drying filters, the air passed through glass wool filters, made by filling ordinary 1-liter, wide-mouthed wash bottles with glass wool. Tests of the air, made by bubbling the supply from these filters through a methyl-orange solution for a period of 30 minutes, indicated that no sulphuric acid passed into the final delivery pipe.

The untreated air entered the final delivery pipe after passing through a glass wool filter. The wet air passed from the glass wool filter through two 2-liter aspirator bottles filled with crushed pumice impregnated with distilled water. To test the evaporating power of the three kinds of air, Livingston ('06, '08, '10a, '10b, '11; see Abbe, '08) cup *atmometers* (evaporimeters) were used. Small Whitehall Tatum museum jars, similar to those used for the sulphuric acid filters, 19 cm. deep inside, and 9 cm. in diameter at the neck, were used to confine the atmometers. The atmometers were placed in position, after being stoppered with one-holed rubber stoppers with small tubes inserted. A large stopper with three holes was used to carry all the apparatus inside the jar. The tubes which connected them with burettes, where the amount of water evaporated was read off, passed through the central hole of the large stopper. Another tube which connected with the air supply passed through one of the side holes, parallel with the evaporimeter and reached within about 5 mm. of the bottom of the jar. The apices of the evaporimeter cups were from 25-30 mm. from the bottom. The third hole in the stopper was used for the exit pipe; the air from the supply passed upward to the bottom of the jar, which was inverted, and in returning to the exit tube, passed over the atmometer. The size of the jar was such that the velocity of the air over the atmometers was the same for a given flow, as across the cages. An atmometer thus enclosed was provided for each of the three kinds of air. For testing relative humidity (Fig. 1C), two long chemical thermometers, graduated to 0.1 of a degree, were inserted inside of a glass tube 50 cm. long and 22 mm. in diameter. One of the thermometers was provided with a wick of absorbent cotton toweling, which dipped into a vial of water. Air from a supply pipe could be introduced into the tube below the bulbs.

Two glass Y's were inserted between the filters and the experimental box, in each air line. The respective stems of these connected with the main air tube and with the experimental cage, as indicated in Fig. 1. One arm of the Y of each line was connected permanently with one arm of the Y attached to the experimental box and supplied with a pinch-cock. The six free Y arms were supplied with free rubber tubes as shown in Fig. 1. The three of these connected with the nearest filters could be joined to the observations tubes (Fig. 1), or to the atmometers, or the thermometer tube. The other three (*FT*) could be used to connect the experimental cages directly with *T* of the control tube to give a rapid flow or when a coil of aluminum pipe submerged in hot water was interposed, to give warm air. These six free tubes made possible cross connections and the shifting of any kind of air to any section of the experimental cage. All open tubes were closed by means of pinch-cocks.

For studying details of behavior and testing the ability of the animals to withstand high rates of evaporation, three glass tubes, each with a total length of 21 cm. and an inside diameter of 32 mm., were used. These were connected with the free rubber tubing of the less frequently used arms of the Y's by means of funnels of the same diameter as the inside of the tubes. The stems of these were inserted into single-holed rubber stoppers. The large end of the funnel was covered with a screen whose meshes were 1 mm. square, and the whole inserted inside the tube, with the stem projecting outside the rubber stopper for the attachment of the rubber tube. The funnel permitted the expansion of the air so as to practically fill the tube when it entered, and the screen prevented the small insects from entering the rubber hose. The air left each tube through the small funnel, similarly inserted into the other end. Since animals find difficulty in walking on curved glass sur-

faces, the lower third of each tube was filled with paraffin upon which sand was sifted while the paraffin was still warm. From each of the tubes the air passed to an atmometer chamber, as previously described, so that the evaporation could be recorded while the animals were being observed.

In order to vary dryness only, it was necessary that the flows of the three kinds of air be the same. The flows were measured by collecting the air for a period of five seconds in a jar filled and inverted in a vessel of water. The pump commonly delivered air under sufficient pressure to force it through the filters and give a flow of from 12 to 16 liters per minute, an amount sufficient to change the air in the part of the cage immediately in front of each introducer (when all are flowing, in the entire cage) in a maximum of .6 of a second.

It was possible to adjust the flows so that they were essentially alike, without collecting the gas. The boundaries of the rear walls of the cages were of solid metal and the slit was midway between top and bottom. A small triangle of thin paper 2 to 3 cm. long and about 1 cm. across the base was taken between the thumb and fore-finger by the point. With the hand held firmly by resting against the cage, the paper was placed in a position such that it was entirely in contact with the upper half of the rear wall without bending. The piece of paper was then lowered so that the broad end came in front of the slit and the deflection of the paper was noted and the flows adjusted until each gave the same deflection. The maximum flow was barely sufficient for effective experiments.

The atmometers were those furnished by the *Plant World*. Three were selected with the standard .75 and restandardized by the careful adjusting of the flows until they were exactly alike. The evaporation was recorded for standard lengths of time when the flows of the medium and dry air were turned alternately over each of the atmometers for several periods of ten minutes and one period of an hour. It was found that the evaporation of one kind of air was the same no matter which evaporimeter was used. At the end of the experiments, the atmometer used with the wet air showed smaller evaporation due in part to sand that was accidentally blown out of the observation tube onto the atmometer.

III. MATERIAL.

The following species were studied: the yellow-margined millipede (*Fontaria corrugate* Wood), ground beetles (two species of *Pterostichus*), the wood frog (*Rana sylvatica* LeC.), the red-backed salamander (*Plethodon cinereus* Green), the sticky salamander (*Plethodon glutinosus* Green) and several species of snails, all from moist forest situations, maximum evaporation is about 11.5 c.c. per day near the surface of the ground; the common toad (*Bufo lentiginosus* Shaw), the digger wasp (*Microbembex monodonta* Say), the bronze tiger beetle (*Cicindela scutellaris lecontei* Hald.), the spiders (*Geolycosa wrightii* Em. and *pikoi* Marx), all from dry sand ridges covered with cottonwoods and pines, a type of situation where the maximum evaporation per day is about 32.5 c.c. The animals were kept in the laboratory under

as nearly natural conditions as possible. With the exception of *Plethodon* and *Fontaria*, they were kept only a few days.

IV. EXPERIMENTAL RESULTS.

1. *Dry Air.*

The air used in the experiments was dried in the sulphuric acid filters described on page 82. The water vapor present after treatment depended upon the humidity of the original air, upon the temperature, the rate of flow, and the number of filters used. On account of variations in temperature and relative humidity from day to day, it is necessary to either practically saturate all the air with water vapor or to dry all of it and follow by standard treatment at a constant temperature if the same conditions are to be produced from day to day. Tables I. and II. (pp. 88, 96) show from 0.5 to 1.05 c.c. evaporation for 20-minute periods (calculated from 10-minute exposures) and relative humidity of 9 to 20 per cent. for the treated air. The relative humidity of the air used ranged from 40 to 60 per cent. of saturation; the reduction in per cent. of humidity ranged from 34 to 52. The moist air was more constant and the evaporation is arbitrarily given as 0.02 c.c. per 20 minutes. This number is based upon a number of one-hour exposures of the atmometers, as readable results were not noted in 10-minute exposures.

(a) *Moist Forest Animals.*

1. *Physiological Effect and Reactions.*—With the exception of the snails the dry air was stimulating to all the animals tried. *Plethodon cinereus* was stimulated at once in the driest air and usually moved back and forth in the observation tubes. Activity sometimes alternated with short periods of coiling but movement was the rule and was usually increased during the first fifteen minutes when erratic movements occurred. These were usually followed by coiling or cessation of activity accompanying a dry appearance of the skin. The animals usually dried and shriveled without further activity, the ability to move being gradually reduced. In the medium air, when the rate of evaporation was low, they often behaved quite normally for a few minutes when

coilings and activity began to alternate. This was followed by heightened activity and stiffening as before. In the gradient a negative reaction to air of more than a minimum evaporating power was clearly shown as indicated by Table I., and Chart I., Experiment II (p. 87). The salamanders appeared to sense the drier air at once as indicated by hesitation or by turning back when the change was encountered. The latter indicates that these animals have a sense of orientation in the gradient. They usually tried the driest air one or more times and the different trials were usually followed by turning when it was encountered again. They usually piled together in the moist air after 13 to 18 minutes and remained so for considerable periods. *P. glutinosus* is clearly more sensitive to dryness than is *P. cinereus*. While the former was clearly more stimulated in both observation tubes and gradient experiments than was the latter, stiffening due to drying appeared so early that in the gradient experiments *glutinosus* did not turn back as definitely as did *cinereus*.

The wood frog was stimulated at once in the dry air; it showed agitation at first but very soon (a few seconds to five minutes) crouched close to the bottom, drew the legs close to the body, and partially or wholly withdrew and closed the eyes. After this had continued for a time, the frog usually hopped in the direction in which it was headed and if the disturbance was not relieved it repeated the crouching.

While the frogs sometimes appeared to orient in the gradient, this capacity is poorly developed and the graphs are quite different from those of the salamanders. The frogs showed a preference for the moist air and avoided the dry air mainly by random hops and a lesser tendency to hop in the moist air. The difference in the appearance of the animals in the different parts of the experimental cages was striking. In the air of highest and medium evaporating powers the withdrawal and closing of the eyes just referred to took place to a degree apparently proportional to the rate of evaporation. Here the skin was dry and dull. In the moist air, the difference after a few moments exposure, was striking. The skin glistened with moisture, the frog sat upright, the eyes were fully protruded and wide open, and the animals gave an impression of sagacity not

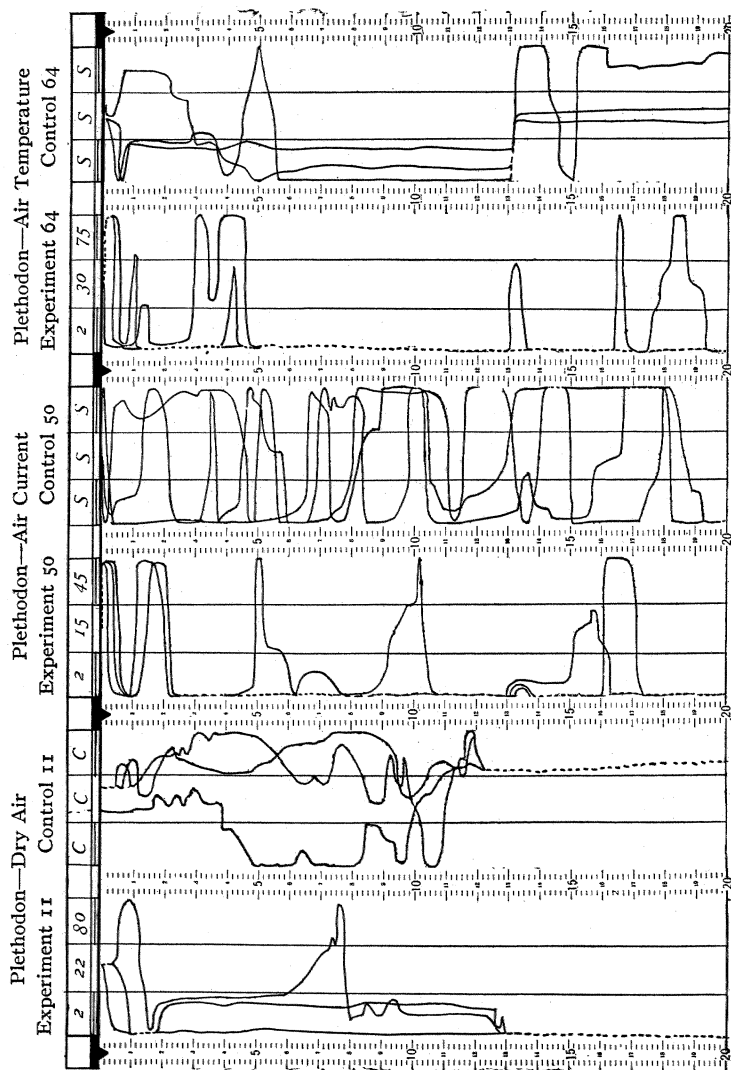


CHART I. Showing similarity of reaction of *Plethodon cinereus* to high evaporation due to dryness, current and higher temperature. Distance from right to left between the scales represents the length of the cage. The vertical scales are time scales with minutes divided into ten second periods. The tracings represent the movements of the individual animals; horizontal distance represents distance lengthwise of the cages and vertical distance represents time. The solid vertical lines separate the divisions corresponding to the thirds of the cages. The numbers at the heads of these columns in the experiments represent the evaporation in hundredths of cubic centimeters during the 20 min. experimental periods. In the controls the letter C indicates that a current was flowing while S indicates standing air. The similarity of the negative reaction to the highest evaporation is clear in the three cases; the avoidance of it was least in the experiments where the evaporation was least rapid. The control of Expt. 11 shows the typical bunching of the individuals in conditions of considerable evaporation.

TABLE I.

Showing the reactions of moist forest animals to gradients of evaporating power produced by different amounts of atmospheric moisture. Flow 12 to 16 liters per min. Three individuals were used. The experiments bearing a number and the letter A were performed with the individuals used in the experiments bearing the same number without the A:—e. g., the control individuals of 5 were used in expt 5A, etc. The experiments lasted 20 min. except where B and C appear. These experiments lasted 40 min. or an hour; 9B is the 2d, 20 min., 9C the third. Averages of the controls are averages of all controls including those shown in tables IV and VI. Experiments starred were performed with E. O. Deere. Length; *Rana* 2 to 3 cm.; *Plethodon* 5 to 8 cm.

No. of Experiment.	Species.	EXPERIMENT.						CONTROL.					
		Evaporation in c.c. During Experiment.			Relative Humidity in Per Cent. of Saturation.			Turned Back From		Per Cent. of Time in Thirds.			Temperature of Control.
		Moist.	Medium.	Dry.	Moist.	Medium.	Dry.	Moister.	Dryer.	Moist.	Medium.	Dry.	
5*	<i>P. cinereus</i> (duplicate control).	0.02	0.40	0.80	—	—	—	2	5	82	14	4	26
5A*		0.02	0.40	0.80	—	—	—	8	14	63	28	9	26
5X		0.02	0.22	0.80	98	56	20	1	5	93	5	2	22
57		0.02	0.40	0.90	98	61	9	0	2	75	21	4	21
4*		0.02	0.25	0.60	98	54	16	0	8	86	9	5	21
Average:		0.02	0.33	0.78	98	57	15	2	7	80	15	5	23
58	<i>P. glutinosus</i> <i>Rana</i>	0.02	0.30	0.80	98	60	10	0	7	91	7	2	22
60		0.02	0.30	0.60	—	—	—	0	0	33	45	22	22
7*		0.03	0.30	0.75	96	54	16	0	1	72	26	2	22
10		0.03	0.30	0.90	96	56	19	0	0	82	18	0	24
59		0.02	0.45	0.50	—	—	—	0	0	65	20	15	22
6*	<i>Rana</i>	0.02	0.25	0.50	98	54	16	1	2	74	12	14	21
6A*		0.02	0.25	0.50	98	54	16	2	2	41	28	31	21
Average:		0.02	0.31	0.74	97	55	17	0.4	2.4	66	22	12	22
								1	1	36	30	34	22

TABLE I.—Continued.

No. of Experiment.	Species.	EXPERIMENT.						CONTROL.											
		Evaporation in c.c. During Experiment.			Relative Humidity in Per Cent. of Saturation.			Turned Back From		Per Cent. of Time in Thirds.		Temperature of Experiment.	Turned Back From		Per Cent. of Time in Thirds.			Temperature of Control.	
		Moist.	Medium.	Dry.	Moist.	Medium.	Dry.	Moister.	Drier.	Moist.	Medium.		Dry.	Corresponding to Moist.	Corresponding to Drier.	Corresponding to Moist.	Corresponding to Medium.		Corresponding to Dry.
9	<i>Fontaria</i>	0.02	0.30	0.90	98	56	19	I	2	47	21	32	24	0	0	39	17	44	24
9B		0.01	0.30	0.90	98	56	19	I	2	67	16	17	24	0	I	46	21	33	24
9C		0.01	0.20	0.60	98	56	19	I	1	55	16	29	24	1	I	45	23	32	24
12		0.02	—	0.50	—	—	—	I	2	62	25	13	20	2	I	38	26	36	20
56		0.02	0.45	0.90	98	61	9	0	3	48	22	30	21	4	I	46	19	35	21
62		0.02	0.45	0.60	98	46	12	2	3	54	17	29	24	2	I	21	16	63	20
Average:		0.02	0.34	0.73	98	55	15	I	2.3	56	19	25	24	1.2	.9	39	21	40	22
14	<i>Carabid</i>	0.02	—	0.75	—	—	—	2	7	80	15	5	20	I	I	56	7	37	20

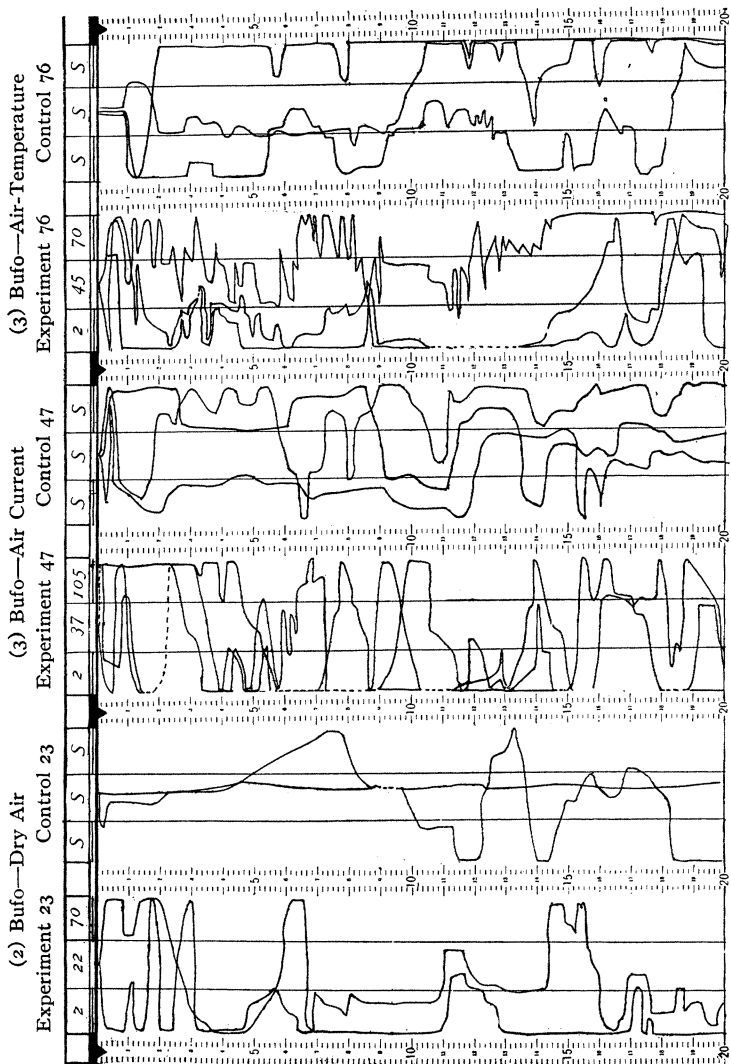


CHART II. Shows the negative reaction of *Bufo* to air of high evaporating power. The avoidance of the dry and moving air is clear. The reaction to the hot air is marked by peculiar short back and forth movements and the avoidance was a little less sharp than in the other cases. Comparison of this chart with Chart I. (p. 87) gives a good idea of the relative avoidance of the same or similar conditions by two amphibians that usually spend the day under cover and come out on cloudy days and at night. The difference is associated with habitat preference.

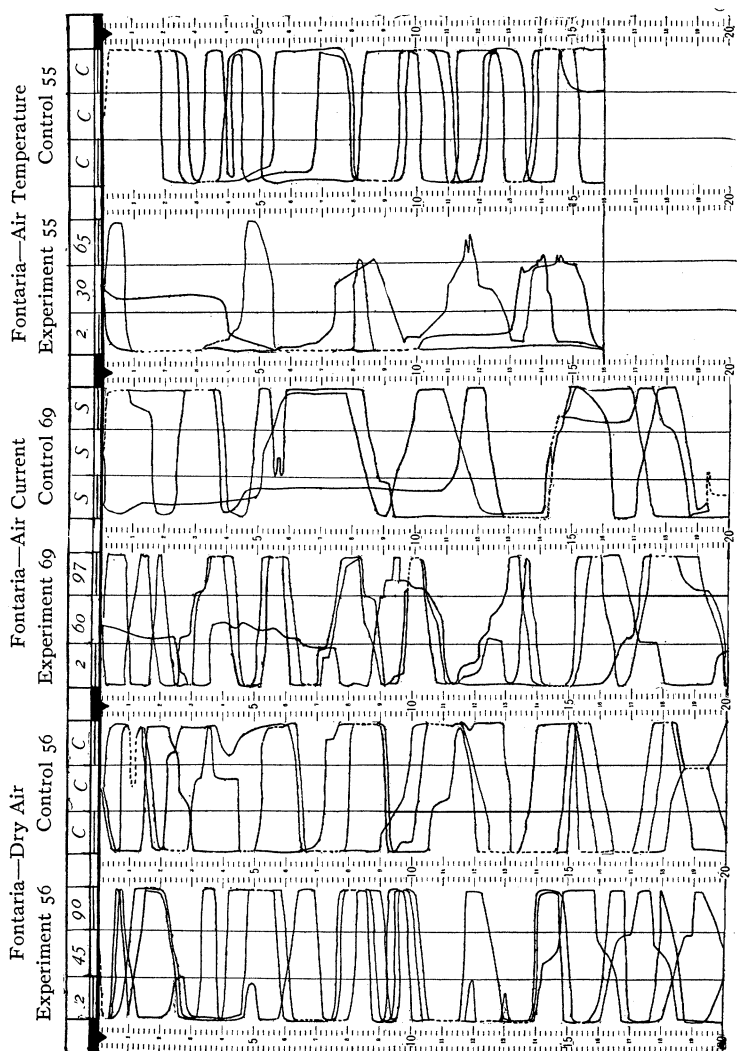


CHART III. Showing similarity of reaction to current and dryness and a sharper reaction to temperature in experiments with *Fontaria*. The small number of turnings from the dry and moving air is evident; turnings are replaced by hesitation at the boundary of the highest evaporation rate and short stays in the dry and moving air. The avoidance of the higher temperature is sharp.

belonging to the anurans. In a few experiments with *Chrophilus nigrinus*, it was found that this frog possesses a similar set of reflexes.

The ground beetles (*Pterostichus adoxus* (1) and *pennsylvanicus* (2) were very sensitive to the dry air, *P. pennsylvanicus* particularly so (Expt. 14, Chart V., p. 97). Here two specimens of *pennsylvanicus* tried the dry air a few times and then began to hesitate and turn back. The individual of *adoxus* was less active but after one trial of the driest air and one turning from the medium, came to rest in the moist air as did the *pennsylvanicus* after a number of trials and turnings and at the end of fifteen minutes. The loss of the stock of *pennsylvanicus* necessitated the repetition of the experiment with *adoxus* alone. In the second trial, the beetles when put in the center dashed lengthwise of the cage once and by chance all bunched together in the driest air, due to thigmotaxis and gregarious tendencies. Soon they became very much stimulated and single individuals dashed to the moist end of the cage and back with great speed. This bunching interfered with the reaction and at the end of the 20-minute period only two had worked out a preference for the moist air.

Fontaria was clearly stimulated by the dry air after less than five minutes exposure in the observation tubes. The individuals in the medium air showed less activity than those in the driest. Individuals in the moist air remained quiet most of the time. In most cases in the gradients (Chart III., Expt. 56, p. 91) the *Fontarias* entered the driest air a number of times and then began to show greater activity in the dry end, to stay a shorter time there, to hesitate upon entering, and to turn back occasionally. Their reaction to the dry air was clearly negative as shown by a time preference for the moistest air, and the haltings and turnings even, though the ability to orient in the gradient seems poorly developed.

Snails and slugs are not good for gradient experiments of short duration because of their sluggishness. The slug (*Philomycus carolinensis* Bosc.) was usually inactive in the moist air but quite active during the first half hour in the dry air. Here the tentacles were withdrawn in less than five minutes and remained so

until death ensued. Inactivity or very slow movements were characteristic of the second, third and fourth half-hour periods. Marked reduction in size was evident in about two hours. They died after two and one half hours.

Comparable results were obtained with several snails. *Polygyra thyroides* Say, when active at the time put into the observation tubes, behaved as follows. In the moist air activity continued intermittently. The animals retreated into the shell from time to time and usually remained stuck to the side of the tube for half an hour or more. In the dry air withdrawal into the shell followed in five minutes but partial extension sometimes continued from time to time during the first half hour. In one individual, a fresh epiphragm was formed at the end of two hours and shrinkage and withdrawal into the shell continued during several hours of observation. *Polygyra palliata* Say behaved similarly. Active individuals put into dry air became inactive but more quickly than *thyroides*. When put into the tubes in an inactive state and with strong epiphragms no activity occurred in either medium or dry air. In the moist air the foot was protruded after 45 to 55 minutes and creeping began after 70 minutes.

On one occasion specimens of several species were taken from the same stock jar and placed in the moist air together, with the following results: *Polygyra palliata* Say and *P. thyroides* Say became active in 10 to 20 minutes, *Pyramidula alternata* Say in 80 minutes, *Polygyra fraudulenta* Pit. showed no activity at the end of three hours and forty minutes but was found moving 14 hours later, a night having intervened. The experiments were carried far enough to show that activity may ordinarily be induced in faint light by air nearly saturated with moisture but it is clear that other factors are concerned because occasionally it is not induced and when so, frequently does not continue.

(b) *Sand Dune Animals.*

Of the sand area animals studied, the common toad is least characteristic of sandy situations because toads belonging to the same species are found in moist woods, and because toads of the dunes breed in the pools and not on the dunes.

Furthermore these toads are probably physiologically different from toads of moister situations. The toads are the only sand animals used that clearly avoided dry air. The stimulation was less marked than that of the wood frogs and was not accompanied by striking or characteristic reflexes. Activity was greater in the controls of gradient experiments where uniform current was used than where still air was used (Chart II., Expt. 23, p. 90). In the gradient the toads were negative to drier air (Table III.) but turned back much less definitely than did the salamanders. Rapid random movements appeared to be characteristic. The ability to orient in the gradient is poorly developed.

The spiders (*Geolycosa*) appeared not to be affected by the moist air. When observed in the tubes, no differences between the individuals in the different conditions could be noted. In the gradient experiments (Table II.) a positive reaction to dry air was clearly shown when the spiders were induced to move about. It was necessary to select individuals of the same sex and of about the same size, as these animals manifested a very striking repulsion for one another and when one spider came near to another one or both darted away with great speed. Thus when one spider moved, three being present, more movement usually resulted and if none of the spiders was killed in combat the experiment resulted successfully. In many cases however, especially when differences in size or sex occurred, some of the spiders usually were killed before the experiment ended. Experiment 29, Chart IV., shows a typical graph characterized by the erratic dashes made by two individuals when meeting.

The digger wasps (*Microbembex*) were likewise slightly positive (Table II.) to dry air, though their chief reaction was digging (Chart V., p. 97). The digging reaction took place in the medium and moist air but not in the dry. There was no special activity in the dry air. In Chart V. the reaction of three individuals in a gradient is shown; the crosses indicate that the wasp was digging at the half minute opposite which the cross appears. It will be noted that the crosses are all in the moist and medium sections.

A few experiments were tried with grasshoppers from sand

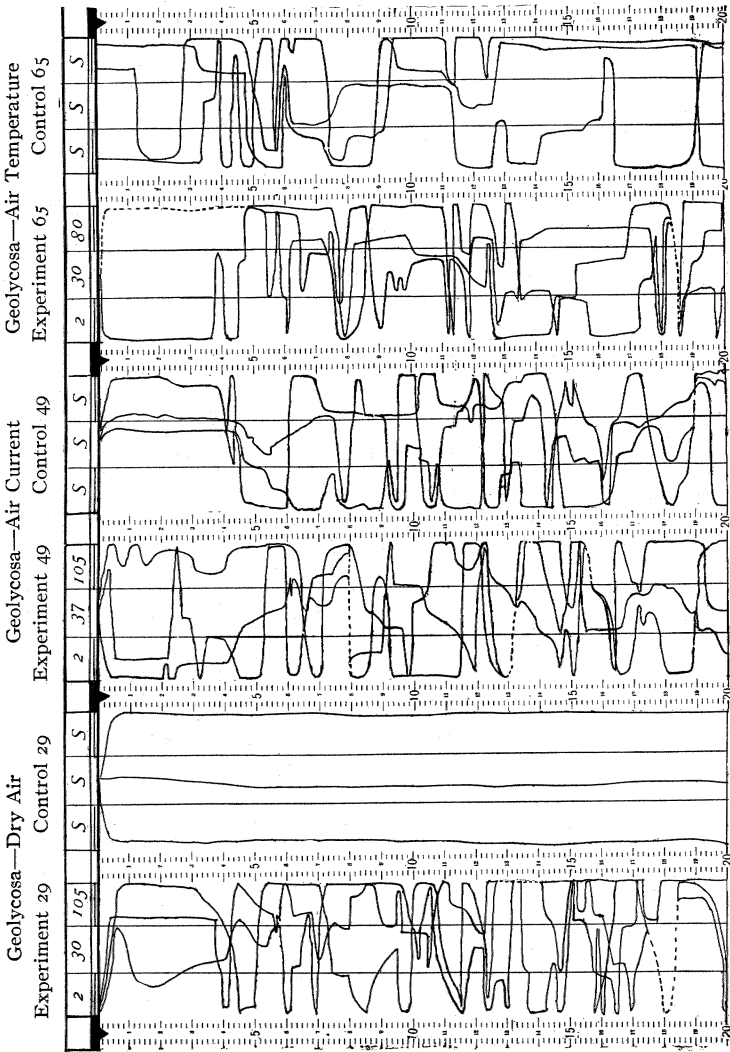


CHART IV. Showing the reactions of *Geolycosa* to air of high evaporating power. An avoidance of the *lowest* rate of evaporation is clear in all cases. A comparison with Chart III. (p. 91) shows the behavior of two Arthropods of roughly comparable habits but different habitat preferences.

TABLE II.

Showing the reactions of cottonwood dune animals to gradients of atmospheric humidity; 20-minute experiments. Flows 12-16 liters per minute. See description of Table I. Averages of the controls are the averages of all the controls including those in Tables IV. and VI. Length: *Bufo*, 2.5 cm.

No. of Experiment.	Species.	EXPERIMENT.						CONTROL.					
		Evaporation in c.c. During Experiment.			Relative Humidity in Per Cent. of Saturation.			Turned Back From		Per Cent. of Time in Thirds.		Temperature of Experiment.	Temperature of Control.
		Moist.	Medium.	Dry.	Moist.	Medium.	Dry.	Moister.	Drier.	Moist.	Medium.	Dry.	
23	<i>Bufo</i>	0.02	0.22	0.67	—	—	—	1	9	66	22	12	20
42		0.02	0.22	0.75	—	—	—	2	6	55	16	29	23
43		0.02	0.22	0.75	—	—	—	11	19	62	31	7	23
61		0.02	0.45	0.90	98	40	10	11	21	50	35	15	24
Average:		0.02	0.31	0.76	98	40	10	6	14	58	26	16	22.5
28	<i>Geolycosa</i>	0.02	0.45	0.75	—	—	—	2	0	24	17	59	20
29		0.02	0.30	1.05	—	—	—	11	17	28	13	59	20
30		0.02	0.30	0.90	—	—	—	0	2	63	28	9	20
32		0.02	0.22	0.81	—	—	—	1	0	58	10	32	19
Average:		0.02	0.32	0.68	—	—	—	3.5	2	43	17	40	20
22	<i>Microbembex</i>	0.02	0.22	0.67	—	—	—	12	10	23	62	15	20
24		0.02	0.30	0.52	—	—	—	14	8	12	46	42	21
26		0.02	0.30	0.60	—	—	—	18	17	30	49	21	21
27		0.02	0.22	0.81	—	—	—	21	16	30	49	21	20
33		0.02	0.22	0.79	—	—	—	5	6	18	54	28	19
34		0.02	0.22	0.81	—	—	—	18	14	32	34	34	19
Average:								14.6	12	24	50	26	20
								7.1	7.6	29	37	34	20

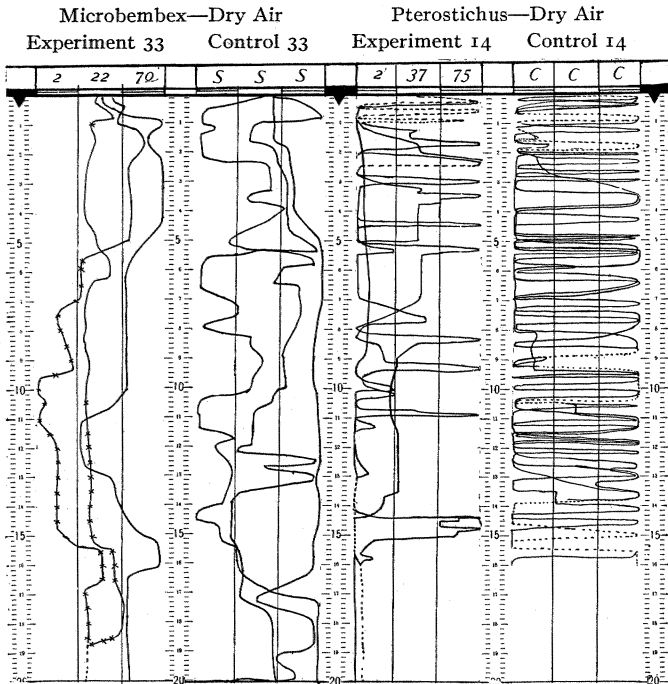


CHART V. Compares the reactions of a diurnal dune animal (*Microbembex*) and a nocturnal beech forest animal (*Pterostichus*). The two differ both in habitat preference and daily habits and the graphs are strikingly different. The crosses in tracings for *Microbembex* indicate that the animal was digging at the half minutes indicated opposite.

areas but they rested in one position, the depth of the cages not being sufficient to enable them to hop. The bronze tiger beetle (*Cicindela lecontei* Hald.) was tried and gave a negative reaction to air evaporating 1.2 c.c. in 20 minutes (3.6 c.c. per hour) and a positive reaction to air evaporating 0.52 c.c. per 20 minutes (1.56 c.c. per hour) produced by heat and current. They were so active that it was necessary to take readings of the number in each third every ten seconds.

2. Rapidly Flow Air.

The rate of evaporation is markedly influenced by rate of flow, and particularly there is a marked difference between a barely measurable movement and a very slight breeze such as .52 meter per second (1.1 miles per hour). Table III. brings

out these relations in a rough way. More accurate results were not easily obtainable because of the difficulty of controlling humidity and temperature and accurately measuring the flows. It will be noted that a doubling of velocity was accompanied by a doubling of evaporation only in the cases of .052 and .104 meter per second. A breeze of .208 meter per second can be distinguished by the skin of the hand but usually lesser flows cannot.

TABLE III.

Showing the relation of evaporation to the rate of flow and to relative humidity under the experimental conditions, together with the relative rate of increase of evaporation and velocity. (.052 meter per sec. equals 1.1 miles per hour, 0.68 equals 1.5; 0.10 equals 0.2.) The equipment is not accurate enough to make this more than a general guide. Pressure was not read.

Approximate Flow in Liters per Minute.	Approximate Velocity in Meters per Sec.	Approximate Evaporation in c.c. per Hour.	Temperature in Degrees C.	Relative Humidity in Per Cent. of Saturation.	Ratios.	
					Increase in Flow.	Increase in Evaporation.
1.9	.012	.25	22.4	50	1	1.0
3.9	.026	.40	22.2	53	2	1.6
7.8	.052	.75	22.2	53	4	3.0
15.6	.104	1.50	22.2	53	8	6.0
31.2	.208	2.00	22.2	54	16	8.0
62.4	.416	2.60	22.2	53	32	10.4
78.0	.520	2.90	18.8	45	40	11.6
15.6	.104	1.4	19.0	35	1	1.0
102.0	.680	3.7	19.0	35	6.5	2.5
15.6	.104	1.6	18.0	45	1	1
31.2	.208	2.3	18.0	45	2	1.4
Average:	.104	1.55	20.1	49	1	1.0
	.208	2.15	20.1	49	2	1.35

Compare with Schierbeck ('95), p. 221. Changes in rate of flow give greater difference in evaporation below .208 meter per sec. than above. Schierbeck's table gives accurate data from .88 m. per sec. to 4.23 m. per sec. for exposed water surfaces (see Livingston, G. T., '08, '09).

(a) *Physiological Effect and Reactions.*

The same species were studied and the same general physiological effects noted as where the difference in evaporation was due to dryness. Only slight evidence of mechanical stimulation occurred in the case of *Fontaria* in the gradient. The salamanders showed the same kind of activity and symptoms of drying in the rapid as in the dry air. The animals pushed

TABLE IV.

Showing the relation of animals to a gradient of evaporating power due to differences in rate of flow. Low evaporation was produced in two ways: (a) by allowing the moist air to drift across the cage at the rate of .026 to .052 meter per sec., marked "wet," and (b) by having no current at all, evaporation given as +.

No. of Experiment.	Species.	EXPERIMENT.						CONTROL.					
		Evaporation in c.c. During Experiment.			Relative Humidity in Per Cent. of Saturation.			Turned Back From		Per Cent. of Time in Thirds.			Temperature of
		Low.	Medium.	High.	Low.	Medium.	High.	Low.	High.	Corresponding to Low.	Corresponding to Medium.	Corresponding to High.	
50 71	<i>Plethodon cinereus</i>	+ wet	.015 .60	.045 .97	47 98	47 56	47 56	0 4	1 8	1 0	31 32	38 68	21 23
Average:			.37	.071		52	52	2	4.5	0.5	15	53	22
51	<i>P. glutinosus</i>	+	.22	.045	66	66	66	0	2	79	10	11	19
52 70	<i>Rana</i>	+ wet	.22 .60	.045 .97	66 98	66 56	66 56	0 0	1 0	19 65	76 20	5 15	19 24
Average:			.41	.071	—	61	61	0	.5	42	48	10	21
48 48A 48B	<i>Fontaria</i>	+	.37	1.05	47	47	47	0 0 0	1 1 0	37 53 40	27 15 18	36 32 42	22 22 22
Average Expt. 48:		wet	.60	.095	98	56	56	0 0	1 3	43 46	21 26	36 28	22 24
69	<i>Fontaria</i>							0	2	45	23	32	22
Average:			.49	1.01		51	51	0	2	45	23	32	22
47 68	<i>Bufo</i>	+ wet	.37 .60	1.05 .97	47 98	47 56	47 56	4 9	10 5	44 71	26 8	30 21	22 24
Average:			.42	1.01		51	51	6.5	7.5	57	17	26	24
49 67	<i>Geolycosa</i>	+ wet	.37 .37	1.05 1.05	47 98	47 47	47 47	9 14	9 9	30 31	25 23	45 46	22 23
Average:			.37	1.05		47	47	11.5	9	31	24	46	22

against the glass cover more often than in the dry air. This occurred in the cases of *Geolycosa* and the salamanders. Table IV. shows a greater degree of positiveness for moist than for still air (see Charts I. to IV., pp. 87, 90, 91, 95, central graphs).

3. Warm Air.

Table V. shows the effect of raising the temperature upon the humidity and evaporation. The difficulty in manipulating this sort of experiment lies in the fact that the atmometers and the water in the burettes *should be at the same temperature as the air used*, if results comparable to those at room temperature are to be obtained. This was accomplished approximately, for the purpose of obtaining the data presented in Table V., but the equipment was faulty and the table is probably only sufficiently accurate to give a general idea of the effect of raising the temperature. A rise of 15° to 17° C. is required to double the evaporation.

TABLE V.

Showing the effect of raising the temperature upon humidity and evaporation under the experimental conditions. Air pumped from a dry greenhouse. Flow 15.6 liters per min.; velocity over the evaporimeters about .104 meter per sec. or 0.2 mile per hour.

Unwarmed Air.				The Same Air Warmed.			
Date.	Temperature in Degrees Centigrade.	Humidity in Per Cent. of Saturation.	Evaporation in c.c. per Hour.	Temperature in Degrees Centigrade.	Temperature Increase.	Relative Humidity in Per Cent. of Saturation.	Evaporation in c.c. per Hour.
Dec. 20	19	37	1.4	30.0	11.0	17	2.0
Jan. 21	14.5	38	1.5	25.5	11.0	19	2.3
Jan. 24	22.6	37	1.6	27.5	5.0	25	2.3
Jan. 24	22.6	37	1.6	32.6	10.1	18	2.7
Jan. 24	22.0	32	1.6	38.0	16.0	14	3.1

(a) Physiological Effect and Reactions.

The effect of increased evaporation due to rise of temperature is more marked than when the evaporation is due to movement or to dryness. This is probably due to the fact that animals are quite sensitive to temperature alone although the temperature of either air or water has rarely been varied alone and a part of its supposed effect may be due to increased evaporation in air or to decrease in gases in solution in water.

TABLE VI.

Showing reaction to evaporation due to higher temperature. Flows approximately 15.6 liters per min. This type of experiment is more difficult than the others and the temperature, humidity and evaporation records are less accurate because the experiments were largely performed before the methods of control were perfected. Averages of controls are averages of all controls including those in the preceding tables.

No. of Experiment.	Species.	EXPERIMENT.						CONTROL.										
		Evaporation.			Humidity.			Turnings From			Per Cent. of Time in							
		Moist.	Medium.	Warm.	Moist.	Medium.	Warm.	Moist.	Medium.	Warm.	Temperature.	Turnings From		Per Cent. of Time in				
										Expt.	Control.	Corre- sponding to Moist.	Corre- sponding to Warm.	Corre- sponding to Moist.	Corre- sponding to Medium.	Corre- sponding to Warm.		
54	<i>P. cinereus</i>	0.02	0.35	0.55	98	61	26	0	7	43	9	32	22	5	6	56	30	
64		0.02	0.35	0.75	98	40	35	1	5	88	4	32	22	0	1	61	22	
Average:		0.02	0.35	0.65	98	50	30	0.5	6	65	28	7	32	22	2.8	2.5	36	28
73	<i>Rana</i>	0.02	0.45	0.60	98	43	34	0	6	93	5	2	31	22	1	1	9	52
77		0.02	0.45	0.60	98	43	36	2	4	35	46	19	29	24	0	2	36	30
Average:		0.02	0.45	0.60	98	43	35	1	5	65	25	10	30	23	1	1	36	30
75	<i>Fonlaria</i>	0.02	0.30	0.52	98	44	43	0	6	69	22	9	32	22	1	2	38	23
55		0.02	0.45	0.65	98	61	29	1	6	66	29	5	29	23	1	0	42	16
Average:		0.02	0.37	0.56	98	52	31	0.5	6	68	25	7	30	22	1.2	0.9	39	21
72	<i>Bufo</i>	0.02	0.45	0.60	98	43	36	0	3	87	1	12	29	23	13	9	21	45
74		0.02	0.45	0.60	98	43	36	9	13	36	31	33	29	23	8	15	25	23
76		0.02	0.45	0.70	98	43	34	24	28	51	22	27	29	24	13	13	21	32
Average:		0.02	0.45	0.60	98	43	36	16	14	58	18	24	29	23	8.0	8.1	28	34
65	<i>Geolycosa</i>	0.02	0.30	0.80	98	40	35	9	9	16	32	52	29	23	1	3	30	20
79		0.02	0.45	0.60	98	43	36	15	14	38	23	39	29	23	1	1	35	29
Average:		0.02	0.37	0.70	98	41	35	12	12	27	28	45	29	23	1.8	1.8	29	29

Plethodon cinereus is quickly affected and over-stimulation and coiling appear within one minute while in the dry and rapidly moving air from two to ten minutes are required to bring about the same result. All the activities and symptoms of loss of water are the same as in the dry air (p. 86). In the gradients (Table VI.) one of the graphs shows less clear avoidance of the hot air due to over-stimulation and some loss of correlation in movement. Otherwise the reactions were entirely similar. No temperature experiments were performed with *P. glutinosus* but the difference in behavior in hot and dry air in the tubes was comparable to that of *cinereus*.

Rana behaved exactly as in the dry air in the experiments, with only five degrees increase, but the graph of the gradient experiment with ten degrees difference is like that of *Plethodon* as a very clear orientation occurred.

Fontaria showed the greatest difference when compared with the dry air. The activity was much greater in the hot than in the dry or moving air. Movement in the tubes was increased six times with an increase of 8° C. In the gradient a distinct orientation occurred, the animal turned back upon encountering the hot air. This was a decided difference from the reaction to dry and moving air (compare graphs of Chart II., p. 91).

Some of the toads showed stimulation in the hot air. Activity was increased in the tubes and in the gradient experiments some of the individuals tended, to hop back and forth in the warm end (Chart II., Exp. 76) and only a weak negative reaction resulted. The detailed behavior of *Geolycosa* was not markedly affected by the difference in temperature and a slightly positive reaction was given. *Cicindela lecontei* was likewise positive in the gradient (see Table VII.) but in the tubes showed a greater tendency to "clean" the legs and antennæ while in the hot air.

4. Death through Evaporation.

All of the animals studied may be killed by loss of water. The results are given in Table VII. It will be noted that where records of size were preserved, the smaller animals died from loss of water much more quickly than the larger. This is perhaps due to the fact that the surface is greater in proportion to the

TABLE VII.

Showing the relative length of time and the relative amounts of evaporation required to kill the species used in the experiments.

Species.	No. of Experi- ment.	Method.	High Evaporation.			Medium Evaporation.			Low Evaporation.			Remarks.
			Evaporation in c.c.	Time in Min- utes.	Length in cm.	Evaporation in c.c.	Time in Min- utes.	Length in cm.	Evaporation in c.c.	Time in Minutes.	Length in cm.	
<i>Plethodon cinereus</i> ..	16	Dry.....	3.0	75		*1.4	160		0.7	160		
" ..	16	"	2.3	65								
" ..	82	"	5.5	65		1.0	60		1.5	60		
" ..	97	"	1.7	40	4.2	*0.7	25	4.2	†0.2	25	4.0	† Experiment started at noon. Died 10 A.M. next day in the tube; no current.
" ..	97	"	1.8	45	6.0	*1.2	45	6.0				
" ..	97	"				*2.1	75	9.0				
Average		age	2.8	58		1.3	73					
<i>P. cinereus</i>	97	Wind.....	0.7	15		0.2	15		0.07	15		Medium did not die.
" ..	87	Hot (10°)										10 min. obs.; none killed.
" ..	88	" ..	0.5	23		0.1	20		0.0	20		
<i>P. glutinosus</i>	95	Dry.....	2.4	34	{ 4 to 7							
" ..	98	"	5.4	160			*27					
Average		age	3.9	87								
" ..	93	Wind.....	1.3	30								
" ..	89	Hot (8°) ..	0.07	5								
<i>Rana</i>	15	Dry.....	4.8	155	2	2.2	275	2	0.15	155	2	} Lengths from nose to end of urostyle.
<i>Bufo</i>	95A	"	5.4	160	5					2,220		
<i>Pterostichus</i>	100	"	31.0	1,300								
<i>Fonlaria</i>	100	"	38.0	1,800								
" ..	100	"	40.0	1,860						2,220		
Average		Font.	39.0	1,830								
<i>Geophyosa</i>	100	Dry.....	42.0	2,220						2,220		

volume in the smaller animals. We note further that the animals die after a smaller amount of evaporation when the rate is slow than when it is more rapid. Since the loss in weight of the animals was not determined, it is impossible to state whether it is directly due to differences in the rate of evaporation from the animal and from the atmometer, or to concentration of the body fluids beyond a point compatible with life which resulted in death after a time no matter whether evaporation continued or not. It was noted that after the skin had become dry, the amphibians did not recover even when put into water. However the most remarkable fact brought out by the table is that the animals died more quickly from evaporation due to rapid movement of air than due to dryness. The same is true of evaporation due to higher temperature. *Bufo* survives longer than *Rana*. Of the arthropods *Pterostichus* (ground beetles), *Fontaria* and *Geolycosa* die in the order mentioned. The beetles died 22 hours after the beginning of the exposure.

V. GENERAL DISCUSSION AND COMPARISON.

The general problems involved in the results which have just been presented are among the more complex of physiology. The relations of the various species studied to their environments; the relation of kind of integument to survival time in dry air; and the question of reaction and irritability make necessary a rating of the different species and a discussion of the results of previous workers on the physiology of water starvation.

1. *Rating of the Species Studied.*

In order to make comparisons it is necessary to estimate the degree of avoidance of air of the high or low rate of evaporation. In the main there are two indications of reaction; (a) *time spent in the two kinds of air (halves of the cages)* and (b) *number of turnings back, upon encountering the avoided air*. When both are expressed in terms of per cent. of total and the two regarded as of equal value, ratings can be obtained as indicated in Table VIII. (Shelford and Allee, '13). Since the ratings are based upon a small number of experiments, they can be taken only as tentatively representing the relations of the animals to the rates of evaporation.

TABLE VIII.

Showing the rating of the different species studied when the turnings back from the modified air and percent of time in the two halves of the experimental cages are regarded as of equal value. The ratings are obtained from the percent of total turnings from the halves and the percent of time in the halves. The differences between the two percents in each case were added and divided by 2. When the greatest number of turnings is from the end in which least time was spent the turnings and time are of the same sign (+ or -).

Species.	Controls.		Experiments.						Average			
	Number.	Rating.	Evaporation Produced by									
			Dryness.		Movement.		Temper- ature.				No. Expts.	Rating.
			No. Expts.	Rating.	No. Expts.	Rating.	No. Expts.	Rating.				
<i>Plethodon cinereus</i>	10	± 3.0	5	-71	2	-66	2	-82	9	-73		
“ <i>glutinosus</i>	2	± 7.0	1	-88	1	-82	—	—	2	-85		
<i>Pterostichus</i>	1	± 11.0	1	-72					1	-72		
<i>Rana sylvatica</i>	19	± 1.5	5	-68	2	-80	2	-69	9	-72		
<i>Fontaria corrugata</i>	10	± 6.0	6	-43	4	-55	2	-83	12	-60		
<i>Bufo lentiginosa</i>	9	± 8.0	4	-46	2	-23	3	-27	9	-32		
<i>Microbembex</i>	6	± 1.3	6	+ 6					6	+ 6		
<i>Geolycosa</i> sp.....	7	± 10.0	4	+18	2	+16	2	+12	8	+15		

2. Comparisons.

(a) *Integument*.—An inspection of Table VII. shows that the animals killed by rapid evaporation fall into two distinct groups: (a) those dying with an evaporation varying from 0.07 to 5.40 c.c. after an exposure varying from five to one hundred and sixty-five minutes, and (b) those dying with an evaporation of 31.0 to 42.0 c.c. after an exposure of from 1,300 to 2,200 minutes. The first group is made up of soft-skinned amphibians, the second of chitin-covered arthropods. Even though the arthropods were much smaller (Hill, '06, p. 267) they lived from eight to four hundred and fifty times as long as the amphibians. The loss of water through a tracheal system should be at least as great as through lungs; the difference is probably primarily due to the character of the integument.

(b) *Reaction, Survival-Time, and Habitat Preference*.—A comparison of Tables VII. and VIII. shows that in general there is a rough relation between survival time and reaction among animals

with *similar integuments*. Of the amphibians, the *Plethodons* died in dry air in 58 min. (*cinereus*) and 87 minutes (*glutinosus*) and are rated respectively at - 72 and - 85; *Bufo* died in 160 minutes and is rated at - 32 (compare charts I. and II.): Of the chitin-covered animals *Pterostichus* (Chart V.) is rated at - 72 (single experiment) and died in 1,300 minutes; *Fontaria* at - 60 died in 1,830 minutes; *Geolycosa* rated at + 15 died in 2,200 minutes (compare charts III. and IV.).

The ratings given in Table VIII. clearly fall into two groups which are habitat groups. The *Plethodons*, *Fontaria* and *Pterostichus* were taken from the surface of the ground under the leaves and in a primeval beech forest; *Geolycosa* and *Microbembex* (+ 6, see Chart V.) are regular residents of the driest open sand areas. The toad is an incidental resident of the sand area. A comparison of Tables VII. and VIII., shows that while a relation exists between habitat and survival time it is confined to animals with similar integuments. No such relation exists when one entire habitat is compared with the other habitat group. Omitting the toad, we find that the regular breeding residents of the two habitats (beech woods and open dunes) differ in sign and degree of reaction in a manner comparable with the difference in physical conditions of the habitats (Shelford, '12b). Distribution is then not a life and death matter for adults but a matter of behavior reaction (Shelford, '11, '12a, '12b; Shelford and Allee, '12a, '12b).

A further comparison of the different species given in the table shows important relations to vertical conditions of forest developmental stages (Yapp, '09; Sherff, '12; Shelford, '12a; Fuller, '12). The wood-frog spends much of its time during the day hopping about the forest floor. *P. cinereus* lives more of the time beneath the leaves and is clearly more sensitive to evaporation. *P. glutinosus* occurs in the beech woods proper in numbers only in moist seasons; ordinarily it is confined in ravines where Fuller ('12) found the average evaporation per day for the season to be 1.5 c.c. less than at the surface of the forest proper. Since *glutinosus* occurs in moister situations than does *cinereus*, the difference in the sensitiveness of the two species is related to habitat. The habits of *Pterostichus* are not well known; the species studied

appear to be inhabitants of moist woods. *Fontaria* however while living under the leaves of the beech woods is most common in earlier forest stages (Shelford, '12) where the evaporation is 1.0 c.c. or more per day greater. It is clearly less sensitive to evaporation than *Pterostichus*. *Microbembex* and *Geolycosa* are confined to open sand situations.

3. *Physiology of Water Withdrawal and Water Starvation.*

Tiedeman ('36) described the symptoms of great thirst experienced by travelers in the desert. The first thirst is followed by dryness and smarting of the throat; next the respiratory action is increased and later long deep breaths alternate with hiccoughs; hoarseness occurs and is followed by loss of speech; the pulse is quickened; the skin becomes dry; the muscles become weak and a feeling of great fatigue ensues with staggering and labored movements. The thirst then becomes maddening and loss of consciousness usually follows. Hill ('06) states that with a loss of ten per cent. of his weight in water, a man usually dies. The study of the phenomena of water starvation dates from the beginning of modern experimental physiology. Some of the early experiments in physiology were water starvation experiments on birds and mammals. Schuchardt ('47, see Northwang, '92a) found that pigeons fed on air-dry grain but deprived of water died in about eleven days. Scheffer ('52, see Northwang, '92a, pp. 275-276) describes some of the symptoms of death by water starvation in pigeons. During the earlier part of the experiment there was great unrest and excitement accompanied by characteristic sounds. This gradually passed off and the animal became quiet and did not notice the surroundings or respond to stimuli. Northwang ('92) summarizes the earlier literature. He studied the dry weight of fat-free tissues of water-starved birds and found that it was increased. He came to the conclusion that death from want of water resulted from the accumulation of splitting products in the cells, due to the lack of sufficient fluid to remove them. The results according to this view should resemble fatigue, which may account for the fatigue symptoms which accompany water starvation. He states that fat animals resist lack of water better than those without fat

because fat can be easily split to yield water. Pernice and Scagliosi ('95) worked upon the histology of fowls which had died of water starvation. They state that atrophy of the adipose tissue, muscles and abdominal organs occurs. There is also congestion and drying of the abdominal viscera. The authors found that the structural elements of the tissues, including the nervous system, had atrophied. They came to the conclusion that the possible water fluctuation of the animal tissues is very small and whenever a cell's water content passes a certain limit, death ensues.

All animals produce some water through the oxidation of the hydrogen in their food. According to Atwater (Hill, '06) man produces about one third to one fourth of the amount of water which he gives off through the skin and lungs. Mathews ('13) called attention to this fact in connection with the adaptation of reptiles to desert conditions. Burger ('07) studied the water relations of the meal worm (*Tenebrio molitor*) when kept in dry air and fed on bran which had been dried at 105° C. He considered that the animals were in essentially absolute dryness. Here they lived for weeks but lost weight. He found however that the per cent. of water in the animals remained practically the same until after death and came to the conclusion that the insect larvæ could not use their food to produce water and so the living substance itself was used. No doubt the food taken produced water but this was not sufficient in quantity. The most important fact brought out was that the per cent. of water remained about the same in spite of the extreme dryness and rapid loss of moisture.

No mechanism to prevent loss of water exists in the common frog; its water demand is supplied through the skin. Durig ('01) found that the common European frog died if the loss of water was rapid when 15 per cent. of the frog's weight was withdrawn. If the drying was slow the frogs could lose 30 to 39 per cent. of their weight in water without dying. When the weight was reduced to 61 per cent. the blood corpuscle count was increased to $2\frac{1}{2}$ times the normal.

We note from the changes in activity due to withdrawal of water, inactivity brought out in the preceding pages, that there

was usually increased activity (period of heightened sensibility) followed sometimes by erratic movements (period of over-stimulation), which was followed by depression, apparent fatigue (the depression period). The first and last periods were always evident. The second in some cases only.

(a) *Heightened Sensibility.*

The irritability of the animals is evidently increased by a small loss of water, as indicated by the periods of heightened sensibility and over-stimulation referred to on page 86. The same phenomenon is shown by the increasing avoidance of the air of high evaporating power after several entrances into this air. The increased sensibility is probably due to the concentration of the blood and tissue fluids. Dr. A. P. Mathews and Dr. Carlson have both informed me that when muscle preparations dry during the usual study, contractions and twitchings result. Clearly the drying of the surface of muscles may not only increase the concentration of the ions but may also interfere with neutrality. In the gradients and in the killing experiments the skin of the amphibians clearly dried slightly in the dry air. The same is probably true of the sense organs and tracheal surroundings of the arthropods. The CO₂ output may be interfered with by the drying (Krog, '03, '04; Winterstein, '12). An increased concentration of CO₂ may be a cause of the increased irritability, as Waller ('96) has found that a very small increase of this substance increases activity of nerves.

Carlson ('06) and Meek ('06) secured decreased vigor of contraction in heart and other muscle preparations by the withdrawal of water by means of sugar and glycerine solutions and increased it by diluting the isotonic solutions surrounding the preparations. The cause of the decreased irritability in the case of water withdrawal by hypertonic solutions, is not so apparent and an explanation is not so easily reached, especially when we consider the fact that *Paramæcium* gives the avoiding reaction when water is withdrawn by sugar solution (Jennings, '06). Still the water withdrawal may have been so rapid that an increase in irritability was overlooked because of its transitory character and only the depression period which follows noted (see below).

In the case of bark beetles Hennings ('07) found that dry air increased metabolism and some of their activities. This is probably true with reference to an optimum, as moist seasons usually favor insects. The problem is a complex one and much data must be accumulated before a solution can be reached. Headlee ('13) found that the rate of metabolism of bugs feeding on succulent plants was not increased or modified by variations in moisture.

(b) *Period of Over-stimulation.*

This probably results from the loss of skin action through drying, in the vertebrates. It took place in the amphibians when the skin became quite dry; it did not occur in the arthropods. Skin respiration is important in most of the amphibians, birds and mammals. Sheffer's pigeons passed through a period of unrest preceding inactivity.

(c) *Period of Depression.*

The period of depression came on gradually in the arthropods. In the case of *Plethodon glutinosus* when the experiments were continued for more than 20 minutes, the animals sometimes came to rest in an apparently fatigued state, in the medium or dry air and died in that position. Durig found that the irritability of the muscles ('01) was decreased (latent period increased) and that rate of conduction of nerves ('02) was decreased in the case of frogs that had lost from 8 to 30 per cent. of their weight in water.

4. *Importance of the Evaporation Rate.*

The work on the physiological effect of evaporation from the bodies of animals, has been confined chiefly to the warm-blooded domestic animals and man. The loss of water from the human body was early noticed by Hippocrates and by Galen. Chalmers (1776), Seguin and Lavoiser (1789-90), Abernathy (1793), and Sharling ('42) all appear to have noted water output from the body or lungs. Weyrick ('62) studied the loss of water from the body, Reinhard ('69) found that the water loss was dependent upon temperature, humidity, wind, velocity and pressure. These factors control evaporation (see also Falck, '72;

Erismann, '75). Rubner ('90a, '90b, '90c) found that the rate of evaporation was of much importance in connection with the factors pointed out by Reinhard, in determining the metabolism, and general heat regulation economy in men and dogs, and with Cramer ('94) the effect of hair covering and of sunlight upon water loss and heat regulation. Schierbeck ('95) discussed methods of measuring the effect of atmosphere upon organisms. He found that the evaporation varies as the fourth root of the wind velocity. His conclusions regarding the measure of climate have been borne out by later workers: "Bei der Beurtheilung des Einflusses eines Klimas auf die Wärmeregulirung des Organismus und bei der Beurtheilung der austrocknenden Wirkung desselben sowohl auf den Organismus als auf leblose Gegenstände ist das Hauptgewicht auf die Geschwindigkeit der Verdampfung zu legen." Wolpert ('98, '99, '02a, and '02b) studied the effect of moisture on laborers, the effect of oiling the skin on water loss, the influences of evaporation upon the skin, and the influence of air movement upon water loss and carbon dioxide production. Up to 25° C. the latter was increased; at higher temperatures decreased. Haldane ('05) worked upon the effect of high temperatures on man and found that the discomfort was due to a rise in the body temperature. The ill effects were partially prevented if the air was kept moving thus increasing the evaporation. Hill ('06) summarizes the important work on the subject of water relations and heat regulation. The heat regulating power of a mouse fails at 24-25° C. (p. 269) in a saturated atmosphere, due to rapid loss of heat, and the animals die from cooling. In man it fails at 29° C. in a saturated atmosphere and if he is active and clothed, he suffers from overheating; at 37° and in the absence of clothing any exertion is practically impossible. In a dry air a man may sit for a time at 100° C. Sutton ('08) states that heat stroke occurs only in a very moist atmosphere (see also Osborne, '10). Aron ('11) working on men and monkeys, found that death from exposure to the tropical sun in the Philippines was not due to any effect of the tropical light (Angstrom, '99; Woodruff, '05; Caskellani and Chalmers, '10), as had commonly been supposed but to an overheating of the body. This could be prevented by shade or by air currents which raised the evapo-

ration. In conclusion he states: "My experiments demonstrate the enormous physiological and hygienic importance of ample water evaporation in the tropics."

Hill states that the increased blood count in mammals in high altitudes and balloon ascensions is due to the transudation of the lymph out of the peripheral vessels from which the sample is drawn. Cronheim ('12) however insists that loss of water through the lungs and through evaporation is the factor; no doubt both are correct in a measure. Reduction of pressure increases evaporation (Nothwang, '92).

While from the standpoint of irritability little has been done there is an excellent experimental basis for a statement of the factors controlling the distribution of warm-blooded animals. The importance of any factor on the distribution of animals is its importance in the life of the animals. From the literature cited and from other literature included in the bibliography it is evident that in the case of mammals temperature data have little significance unless the humidity is known. Neither of these can be interpreted without a knowledge of the pressure, isolation, and wind movement. The experimental foundation for the consideration of all these factors was clearly laid down by Reinhard ('69) and Rubner ('90). The best method of expressing them climatologically was stated by Shierbeck ('95) as the amount of water evaporated. This does not mean that records of the separate factors involved, namely, temperature, pressure humidity, isolation, wind movement, etc., should not be made but rather that the best expression of their combined action is the rate of evaporation.

The striking similarity of reaction and survival time to similar rates of evaporation on the part of the animals regardless of whether due to dryness, heat, or velocity speaks very strongly for the measure of evaporation in connection with cold-blooded animals. It is a noteworthy fact that the relation of warm-blooded animals to climatic factors had been observed (Livingstone, '58) and experimentally studied (Reinhard, '69; Rubner, '90) before Merriam ('90, '94, '98) published his theory of temperature control (see Swain, '05; Craig, '08; Roosevelt, '10; Mathews, '13). He made a most important contribution in his emphasis.

of the breeding period. However there is no good evidence that total temperature above an arbitrary minimum is more significant than is total pressure, total sunshine, total wind movement, or (Walker, '03) total humidity. All must be considered together. Temperature control has "worked" in the mapping of distribution just as any theory whatsoever will work for some species be it concerned with a wandering pole or an Atlantis. The facts and causes of distribution are much more complex than the temperature control assumes. While all facts of distribution are worthy of explanation, the biological processes concerned are of vast importance for they include the most complex problems of biochemistry and life phenomena. The increase in irritability shown by the animals studied, the remarkable water-regulating power of the meal worms, brought out by Berger ('07), the quick regulatory changes of the mammals, and other responses to the physical environment (including the surrounding medium) open many new problems to the biochemist. Our explanation of the phenomena concerned must accord with the facts of relations in nature as well as with the results of the laboratory experiments. Experimental ecological investigations give promise of contributing as much toward the solution of some of the broader biological problems as will the investigation of subjects in fields where speculation has added interest and concentrated attention in years past, and, so far, given us a total progress of questionable significance.

SUMMARY.

1. The animals studied react to evaporation whether it is produced by movement, dryness, or heat (p. 105).
2. The sign and degree of reaction are in accord with the comparative rates of evaporation in the experiments and in the habitats from which the animals were collected (p. 105).
3. The animals of a habitat are in general agreement in the matter of sign and degree of reaction; the minor differences which occur are related to vertical conditions, position of maximum abundance in succession, and kind of integument (pp. 97 and 106).
4. Short exposure to high evaporation increases sensibility to evaporation (pp. 87, 90, 91, 95, and 97 (charts)).

5. In the survival time experiments, heightened sensibility was sometimes followed by over-stimulation and always by depression and apparent fatigue (pp. 109-10).

6. There is a rough agreement between survival time and kind of integument but no agreement between survival time and habitat when a number of different members of a community are taken together (p. 106).

7. The rate of evaporation is the best index of the combined action of wind, temperature, isolation, and dryness of air.

8. Temperature is probably no more significant than moisture, isolation, or wind (p. 112).

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